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Source: *The Journal of Wildlife Management*, Vol. 62, No. 2 (Apr., 1998), pp. 663-673
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3802342
Accessed: 05-03-2015 17:49 UTC

CHARACTERISTICS OF AMERICAN MARTEN DEN SITES IN WYOMING

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Abstract: We examined characteristics of den structures and den sites used by female American marten (*Martes americana*) for natal and maternal dens in the Sierra Madre Range, Wyoming. During 1988–95, we located 18 natal dens (parturition sites) and 97 maternal dens (sites where kits were present exclusive of parturition) used by 10 female marten. Important den structures included rock crevices (28%), snags (25%), red squirrel (*Tamiasciurus hudsonicus*) middens (19%), and logs (16%). Resource selection function (RSF) analysis showed that an individual selection model provided a significantly better fit than a null model or pooled selection model, indicating that the sample of marten selected maternal den sites that differed from random sites, and that individual animals did not select maternal den sites in the same manner. Six marten individually exhibited significant selection for maternal den sites within home ranges. Overall selection coefficients for maternal dens indicated the number of squirrel middens was the most important variable, followed by number of snags 20–40 cm diameter at breast height (dbh), number of snags ≥41 cm dbh, and number of hard logs ≥41 cm in diameter. Selection of natal den sites was also significant via comparison between selection and no-selection models, with number of middens, number of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) >20 cm dbh, and number of hard logs ≥41 cm in diameter the most important variables in descending order of importance. Large logs, large snags, and large, live spruce and fir trees are important characteristics for marten den sites in the central Rocky Mountains. The prominence of middens at den sites suggests red squirrels provide important denning structures as well as prey for marten.

JOURNAL OF WILDLIFE MANAGEMENT 62(2):663–673

Key words: den sites, habitat selection, marten, *Martes americana*, maternal, natal, Wyoming.

The availability of denning habitat is essential to successful recruitment and hence to persistence of marten populations. A number of authors have suggested that the availability of dens may limit the distribution of *Martes* species (Schmidt 1943, Bergerud 1969, Wynne and Sherburne 1984, Thompson 1991, Brainerd et al. 1995), yet very little is known about denning requirements of marten. Exclusive of this study, only 87 American marten dens have been described for North America (see Buskirk and Ruggiero 1994). Careful examination of the literature further indicates that only 1 den clearly was identified as a natal den (parturition site; Hauptman 1979). The other dens were either maternal dens (sites where kits were present exclusive of parturition and identified as maternal dens by observing the parturition site and tracking movements to other den locations), or dens where insufficient information was available to unequivocally determine whether they were parturition sites. Although these observations have generated important information, critical data on natal dens are lacking, and there have been no analyses comparing den sites (habitat surrounding dens) with available habitat. As a result, no study has analyzed den-site selection by the American marten, a sensitive species throughout the western United States, and a management indicator species for the U.S. Forest Service (Ruggiero et al. 1994).

Herein, we describe den structures (the actual features marten denned within) and analyze den-site selection based on 18 natal and 97 maternal den sites used by 10 female American marten. Our objectives were (1) describe structures used for natal and maternal dens, and (2) test the hypothesis that marten select den sites based on structural attributes.

STUDY AREA

The study area covered about 270 km^2 of the Medicine Bow National Forest, centered on the Coon Creek and East Fork Encampment River drainages of the Sierra Madre Range in southern Wyoming. Elevations range from 2,600 to

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3,300 m. Mean annual precipitation averages about 100 cm, with 70% in the form of snow. Principal cover types are lodgepole pine (*Pinus contorta*), which covers about 60% of the study area, and Engelmann spruce–subalpine fir, which covers about 40% of the study area, mostly at higher elevations. Lodgepole pine predominates at lower elevations but also occurs at higher elevations intermixed with spruce and fir. The principal understory species are huckleberry (*Vaccinium* spp.), pinegrass (*Calamagrostis rubescens*), and sedges (*Carex* spp.; Marston and Clarendon 1988). Pole-sized trees (<23 cm dbh) occur on 24% of the 2 main drainages on the study area; larger trees occur on 72% of the area. Rock outcrops and meadows occupy the remaining 4% (Raphael 1987). Portions of the study area were "tie-hacked" (i.e., large trees were removed for railroad ties) in the early part of the century. More recent management activities included clearcutting in small (1–2 ha) patch cuts, primarily in the spruce–fir cover type.

METHODS

We trapped marten during all months of the year except April, when whelping occurred. We used number 205 Tomahawk live traps (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) affixed with a wooden box that contained sawdust for warmth and shelter. Traps were baited with >200 g of beaver (*Castor canadensis*) meat. To attach radiocollars (≤33 g), we checked traps daily and immobilized captured marten with 12–18 mg/kg body mass Ketamine HCL. Animals were handled following guidelines of Bull et al. (1996).

We began monitoring movement patterns of radiomarked female marten in late March, which was near the median whelping date of marten on our study area (17 Apr; Henry and Ruggiero 1994). We used Telonics TR-2 receivers (Telomics, Mesa, Arizona, USA) and either dual H-antennas mounted on a fixed-wing aircraft or a single, hand-held, 3-element antenna for ground locations. We located female marten with radiocollars 2 times/week from a fixed-wing aircraft and ≥2 times/week from the ground. We attempted to locate natal dens when female movement and resting patterns became highly localized. We positioned a remote, telemetry-driven activity recorder at den sites to monitor female attendance patterns (Henry et al. 1997). Continuous occupancy of the site by the female indicated that a natal den site had been located (Henry and Ruggiero 1994). When snow melted, the presence of large latrines and prey remains provided confirmation of natal dens. We monitored the behavior and movements of females with kits daily (occasionally every other day). We confirmed dens via a combination of criteria: female behavior (frequent and consistent movements back to the den as established by activity recorders and other ground-based telemetry), fresh excavations or prey remains at the den, direct contact with kits, or presence of a radiocollared kit.

Marten dens were found within specific structures such as logs or snags. We qualitatively described den structures, measured diameters of trees and logs, and measured the height from the ground to the entrance of each den structure. We classified as middens those dens found in logs and the lower boles of snags that were incorporated into intensive red squirrel feeding sites ≥1 m in diameter.

We quantified characteristics of den sites for natal dens, maternal dens, and 100 random locations via nested circular plots that were 11.3 (0.04 ha) and 15.0 m (0.07 ha) in radius. We used different plot sizes to facilitate integration of data with an ongoing study not reported here. We counted the number of red squirrel middens (defined as intensive feeding sites ≥1 m in diameter) within each 0.07-ha plot and determined the number of hard logs (defined as solid logs ≥2 m long and ≥10% within the plot) ≥41 cm in diameter within each 0.04-ha plot. We estimated percent overstory canopy coverage by averaging concave mirror densiometer measurements taken at a distance of 5 m in each of the 4 cardinal directions around den structures and random points. We measured dbh of trees and snags with Biltmore sticks and dbh tapes. The number of live stems of lodgepole pine and spruce–fir was determined for trees >20 cm dbh within a 15-m radius of the plot center. We counted snags 20–40 cm dbh and >40 cm dbh for the same 15-m plots. These variables represent the primary attributes of late-successional forest in our study area.

Data Analysis

We examined den-site selection using log-linear models for RSF analysis based on sample data where only a small fraction of available resource units are used (Manly et al. 1993). Because marten are territorial, females do not have equal access to denning resources. Therefore, we determined habitat selection for individual females by comparing variables at den sites with the same variables at 10 random points located within each animal's home range (design III, sampling protocol A; see Manly et al. 1993). We determined home ranges with the 95% minimum convex polygon method (Mohr 1947) calculated over all years that each marten was monitored. Home ranges of individual marten varied little among years during the study period (O'Doherty et al. 1997).

We calculated RSFs for maternal den sites of individual females, which resulted in a set of selection coefficients (β_i) for each female. Selection coefficients indicated the weighting of each variable relative to other variables in the log-linear selection model and the direction of selection for the variable (e.g., negative selection or avoidance was reflected by negative values and positive selection by positive values). A variable was significant if its selection coefficient differed significantly from zero. To determine significance of selection coefficients, we used the ratio of the selection coefficient to its standard error and obtained *P*-values for coefficients from the standard normal distribution. We chose variables for the den-site selection analysis based on evidence that these variables were biologically important for marten habitat use and rest-site selection (e.g., Buskirk 1984, Spencer 1987). The variables analyzed were not independent. Therefore, we used an alpha level of 0.05 to determine significance of statistical tests.

Significance of selection for maternal den sites was determined via comparison of the deviance value $\{-2[\log_e(\text{likelihood})]\}$ from a no-selection or null model to that from a selection model for each individual. The deviance value provided a measure of the goodness-of-fit of each model to the data. The resulting statistic, $\text{deviance}_1 - \text{deviance}_2$, approximated a chi-square distribution with degrees of freedom equal to the difference of the degrees of freedom between the models (Manly et al. 1993). Because the test for significant selection was based on comparing the goodness-of-fit of the selection and no-selection models, a lack of significance for selection coefficients within the selection model does not negate significance of the overall model as compared to the no-selection model. The relative importance of variables to selection is indicated by the relative values of the selection coefficients.

We estimated an overall selection function for maternal den sites that incorporated the variability exhibited among females by averaging the selection coefficients from RSFs for each female. Significance of the resulting selection coefficients was again determined by comparing the mean of the selection coefficient divided by its standard error with the critical points of the standard normal distribution.

To determine whether maternal den-site selection was significant, we compared deviance values from a null (no-selection) model, where the coefficients were set to zero, to those from the pooled selection model where selection coefficients were estimated by maximum likelihood from the data. We then compared deviance values from the pooled selection model with those from an individual selection model (where the overall deviance and degrees of freedom were the sum of the individual deviance values and degrees of freedom) following Arthur et al. (1996) to ascertain whether individual marten differed in their selection of maternal den sites. Significantly lower deviance values indicated the model with lower deviance provided the better fit to the data.

Fewer natal dens per female (often only 1 or 2) precluded developing natal den RSFs by individual. To avoid pseudoreplication (Hurlbert 1984) without discarding valuable data, we averaged observations for females with ≥ 2 natal dens and pooled these data across females prior to analysis. We tested for significance by comparing the deviance from the pooled data for the no-selection model with that of the selection model as described above. We extended this analysis by removing variables with low selection coefficients in a stepwise fashion comparing the new deviance values from the reduced models to the full model, and recalculating probabilities from the standard normal distribution at each step. This stepwise analysis allowed us to isolate important variables in the log-linear RSF model.

RESULTS

Den Structures

We identified den structures and measured site characteristics for 18 natal and 97 maternal dens used by 10 female marten (Fig. 1, Table 1). Natal and maternal den structures (n = 115

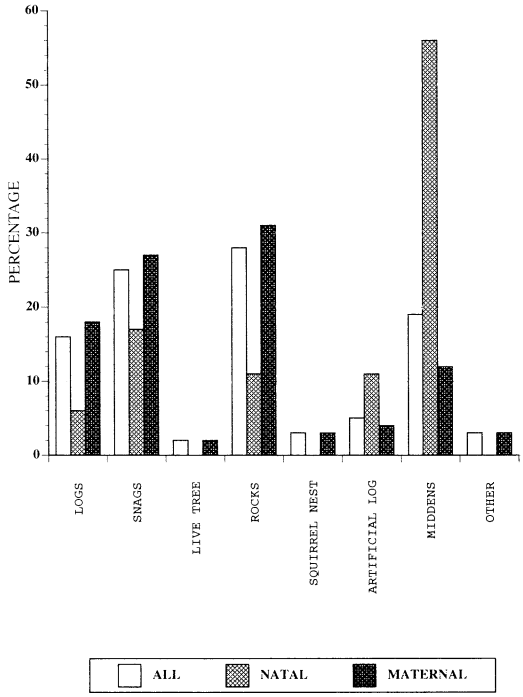

Fig. 1. Natal and maternal den structures used by American marten in the Sierra Madre Range, Wyoming.

dens) included rock crevices (28%), snags (25%), red squirrel middens (19%), logs (16%), live trees (2%), red squirrel nests (3%), artificial log structures (5%), and other (3%; Fig. 1). The category "other" applied to 2 maternal dens: a ground nest and an abandoned burrow of unknown origin. Red squirrel middens were the most common natal den structures (56%; n = 18 dens), and rocks were the most common maternal dens (31%; n = 97 dens). Of the 10 natal dens in middens, 66% occurred in a log, snag, or other structure within the midden. Of the 12 maternal dens in middens, 92% occurred within other structures within the midden. Only 1 log (46 cm in diameter) was used for a natal den. The mean (± SD) diameter of log maternal dens was 53 ± 15.7 cm (n = 17). Three natal dens were in snags that averaged 66 ± 24.6 cm dbh, and 26 snags used as maternal dens averaged 55 ± 13 cm dbh.

Den Sites

The average number of maternal dens per marten was 10.8 (range = 5–24, n = 9; Tables 2, 3). Comparison of deviance values indicated the pooled model provided an improvement over the null model ($P < 0.001$), and the overall individual selection model provided a better fit than the pooled selection model ($P < 0.001$) because of high variability in resource selection among females (Table 2). Comparisons between selection and no-selection RSF models demonstrated that 6 of the 9 females selected structural characteristics for maternal den sites that differed from random sites located within their established home ranges (Table 3). Deviance values of zero for 4 marten indicated the selection model provided a particularly good fit for these individuals. Individual marten differed in den-site selection with regard to structural variables, which was apparent from a comparison of selection coefficients for variables across individuals (Table 2). Selection coefficients were −3.53 to 13.35 for hard logs ≥41 cm in diameter, −14.44 to 5.87 for number of spruce–fir >20 cm dbh, −13.93 to 76.27 for number of snags 20–40 cm dbh, and −13.48 to 32.85 for number of snags >40 cm dbh. Whereas selection coefficients for percent canopy cover and number of lodgepole pine <20 cm dbh were consistently near zero, coefficients for number of squirrel middens were strongly positive for 5 of 9 animals, and positive but near zero for 4 others.

Average selection coefficients for the sample

Table 1. Characteristics of American marten natal den sites, maternal den sites, and random sites within marten home ranges from the Sierra Madre Range, Wyoming.

	Natal dens (n = 18)			Maternal dens (n = 97)			Available sites (n = 100)		
Site characteristics	$\bar{x}$	SE	CV	$\bar{x}$	SE	CV	$\bar{x}$	SE	CV
No. Squirrel middens	1.1	0.33	1.3	0.6	0.11	1.8	0.2	0.07	3.5
No. Hard logs ≥41 cm diameter	4.7	1.31	1.2	3.6	0.39	1.1	2.0	0.32	1.6
% canopy cover	67.4	4.32	0.3	58.2	1.75	0.3	58.2	1.95	0.3
No. Lodgepole pine >20 cm dbh	7.2	1.89	1.1	10.0	1.12	1.1	14.4	1.41	1.0
No. Spruce/fir >20 cm dbh	23.6	3.53	0.6	16.8	1.32	0.8	10.4	1.12	1.1
No. Snags 20–40 cm dbh	2.0	0.52	1.1	3.1	0.26	0.8	1.5	0.17	1.1
No. Snags >40 cm dbh	1.6	0.35	0.9	1.3	0.13	1.0	0.7	0.14	2.0

Table 2. Individual and overall selection coefficients for structural characteristics within 0.04–0.07 ha of maternal den sites for 9 female American marten from the Sierra Madre Range, Wyoming. Sample sizes are in parentheses.

	$\hat{\beta}_i$								
Marten	Number of squirrel middens	Hard logs ≥41 cm diam	% canopy cover	Lodgepole pine ≥20 cm dbh	Spruce–fir ≥20 cm dbh	Snags 20–40 cm dbh	Snags >40 cm dbh	Deviance[a]	df
Null	0.00	0.00	0.00	0.00	0.00	0.00	0.00	273.05	196
Pooled (97)	0.59	0.08	−0.02	0.00	0.00	0.32	0.18	230.67	189
F21 (8)	0.17	0.68	−0.03	−1.21	−0.17	0.22	−0.92	18.85	10
F29 (10)	4.78	11.79	−0.26	1.35	−1.03	−2.87	27.79	00.00	12
F37 (24)	15.31	1.62	0.10	−0.12	−0.19	0.31	−0.61	16.31	26
F49 (17)	0.53	−0.52	−0.07	−0.06	−0.19	1.53	4.64	20.87	19
F53 (5)	96.95	13.35	−2.25	−0.06	−14.44	76.27	32.85	00.00	7
F60 (7)	96.89	8.52	−0.08	0.45	−0.09	19.09	−13.48	00.00	9
F73 (9)	0.00	−0.07	−0.01	0.09	0.16	1.48	−0.10**	14.42	11
F79 (8)	0.00	0.12	−0.14	0.20	0.10	0.79	0.59	15.32	10
F87 (9)	38.39	−3.53	0.16	−2.15	5.87	−13.93	16.53	00.00	11
Summaries for									
$\bar{x}(\hat{\beta}_i)$	28.11	3.55	−0.29	−0.06	−1.11	9.21	7.48		
$SE(\hat{\beta}_i)$	13.64	2.01	0.25	0.31	1.8	8.84	5.04		
P	0.039	0.078	0.250	0.849	0.535	0.298	0.139		
Individual deviance totals								85.77	115
Difference between null and pooled (selection) models								42.38***	7
Difference between pooled (selection) and individual (selection)								144.90***	74

[a] Deviance = $-2[\log_e(\text{likelihood})]$.
** $P < 0.01$; *** $P < 0.001$.

Table 3. Comparison of deviance values for "null" and "selection" log-linear resource selection function models for 9 female American marten from the Sierra Madre Range, Wyoming. Chi-square values and degrees of freedom were obtained by subtracting the selection deviance and degrees of freedom from the null deviance and degrees of freedom. *P*-values indicate the level of significance associated with the improvement of the selection model over the null model. Numbers in parentheses indicate sample size of marten and degrees of freedom associated with the null and selection deviance values.

	Deviance[a]				
Marten	Null	Selection	χ^2	df	*P*
F21 (8)	24.73 (17)	18.85 (10)	5.88	7	0.553
F29 (10)	27.73 (19)	00.00 (12)	27.73	7	<0.001
F37 (24)	41.19 (33)	16.31 (26)	24.88	7	<0.001
F49 (17)	35.59 (26)	20.87 (19)	14.72	7	0.040
F53 (5)	19.10 (14)	00.00 (7)	19.10	7	0.008
F60 (7)	23.03 (16)	00.00 (9)	23.03	7	0.001
F73 (9)	26.29 (18)	14.42 (11)	11.87	7	0.105
F79 (8)	24.73 (17)	15.32 (10)	9.41	7	0.225
F87 (9)	26.29 (18)	00.00 (11)	26.29	7	<0.001

[a] $-2[\log_e(\text{likelihood})]$.

of female marten provided an estimated selection function for the population of females (Table 2). This overall selection function incorporated the individual variability in maternal den-site selection exhibited among females. The selection coefficient from this overall function was significant for number of red squirrel middens ($P = 0.039$) and nearly significant for hard logs ($P = 0.077$). Average selection coefficients for the sample of female marten were highest for number of middens ($\beta = 28.11$), followed by medium snags ($\beta = 9.21$), large snags ($\beta = 7.48$), and hard logs ≥41 cm in diameter ($\beta = 3.55$). Selection coefficients for other variables were near zero.

Comparison between the pooled-selection and no-selection models indicated female marten also exhibited selection of structural characteristics at natal den sites ($\chi^2_7 = 16.68$, $P = 0.020$; Table 4). The number of middens again had the highest selection coefficient ($\beta = 0.64$), followed by spruce–fir >20 cm dbh ($\beta = 0.29$), and hard logs ≥41 cm in diameter ($\beta = 0.13$). Other selection coefficients were near zero, but none of the selection coefficients were significant.

The stepwise reduction of the model did not significantly improve or worsen the fit, with the exception of the comparison of the single-variable model for spruce–fir >40 cm dbh with the full model, which resulted in a poorer fit ($\chi^2_6 = 14.68$, $P = 0.023$; Table 5). However, the model including middens, hard logs ≥41 cm in diameter, spruce–fir >20 cm dbh, and snags >40 cm dbh resulted in significance for number of middens ($P = 0.038$) and number of hard logs ≥41 cm in diameter ($P = 0.008$). Neither spruce–fir >20 cm dbh ($P = 0.153$) nor snags ($P = 0.358$) were significant, but the spruce–fir variable maintained a reasonably high selection coefficient ($\beta = 0.32$); so, snags >40 cm dbh was removed at the next step. For the model with the 3 remaining variables, the only change was that middens was marginally significant ($P = 0.055$). Reduction of the model to number of middens and number of hard logs resulted in a similarly marginal probability for middens ($P =$

Table 4. Resource selection functions for structural characteristics within 0.04 to 0.07 ha of natal den sites used by 10 female American marten in the Sierra Madre Range, Wyoming.

Site characteristics	$\hat{\beta}i$	SE($\hat{\beta}i$)	Error ratio	*P*
No. middens	0.64	0.42	1.53	0.13
No. hard logs ≥41 cm diameter	0.13	0.09	1.43	0.15
% canopy cover	−0.01	0.07	−0.08	0.94
No. lodgepole pine >20 cm dbh	0.06	0.07	0.92	0.36
No. spruce-fir >20 cm dbh	0.29	0.24	1.20	0.23
No. snags 20–40 cm dbh	0.01	0.29	0.04	0.97
No. snags >40 cm dbh	−0.04	0.04	−1.05	0.29

Table 5. Comparison of deviance values and *P*-values from stepwise reduction of the log-linear resource selection function model for structural characteristics within 0.04–0.07 ha of American marten natal den sites in the Sierra Madre Range, Wyoming. Lines connecting reduced models (partial, individual) to the full model indicate a lack of significance between corresponding models ($P > 0.05$).[a]

Structural variables	Full	Partial			Individual		
No. middens	0.126	0.038	0.055	0.056	0.033		
No. hard logs ≥41 cm diameter	0.153	0.008	0.007	0.005		0.003	
% canopy cover	0.936						
No. lodgepole pine >20 cm dbh	0.358						
No. spruce-fir >20 cm dbh	0.230	0.153	0.230				0.147
No. snags 20–40 cm dbh	0.969						
No. snags >40 cm dbh	0.294	0.358					
Deviance	50.34	52.32	53.10	54.48	62.90	57.61	65.02
df	102	105	106	107	108	108	108

[a] Only the individual model for spruce-fir >20 cm dbh differed from the full model ($P < 0.05$).

0.056) and a significant value for hard logs ($P = 0.005$).

The individual models resulted in significance for number of middens ($P = 0.033$) and number of hard logs ($P = 0.003$), but not for number of spruce–fir >20 cm dbh ($P = 0.147$), which produced a poorer overall fit than the full model ($\chi^2_6 = 14.68$, $P = 0.023$). These results suggest that important information was lost by including only number of spruce–fir.

Selection coefficients changed very little during the stepwise analysis. Coefficients increased from 0.64 to 0.72 for number of middens and from 0.13 to 0.20 for number of hard logs ≥41 cm in diameter, and decreased from 0.29 to 0.25 for spruce–fir. The consistency of the selection coefficients during the stepwise analysis supports contentions of Manly et al. (1993) regarding the robustness of RSF to subjective inclusion or exclusion of variables. The stepwise results indicated the number of squirrel middens and the number of hard logs ≥41 cm in diameter were important variables contributing to the significance of the full log-linear RSF model. The lack of significance for number of spruce–fir >20 cm in diameter in the single-variable model suggests the sample size may have been too small relative to its variability, given that its coefficient was larger than that for hard logs, which was significant.

DISCUSSION

Den-Structure Characteristics

Natal den structures included large snags, rocks, and large logs, but marten strongly favored red squirrel middens when choosing parturition sites. Most natal dens, even those within middens, were in secure structures that would seemingly offer protection from a wide range of predators. However, the preponderance of dens in middens suggests that such sites offer more than protection from predation. Red squirrel middens provided the primary resting sites for marten in Alaska (Buskirk 1984), and middens were often associated with resting sites in Montana (Coffin 1994). During winter in California, martens rested in Douglas' squirrel (*Tamiasciurus douglasii*) "cone cashes" associated with decayed wood (Spencer 1987); in Yellowstone National Park, marten used middens as subnivian access points (Sherburne and Bissonette 1993).

Another notable characteristic of marten natal dens was their vertical placement. Several authors have suggested that marten move to dens on the ground after initially denning in elevated structures (Wynne and Sherburne 1984, Clark et al. 1987, Strickland and Douglas 1987). Our findings do not support this conclusion, given that 94% of our natal dens were located in ground-level structures. Only 1 of 18 was >2 m above the ground.

Maternal den structures were more diverse than natal dens and more evenly distributed across the 4 dominant categories (rocks, snags, logs, and middens). Rocks were the most frequently used maternal den structure, accounting for 31% of the 97 maternal dens. Only 2 other maternal rock dens have been observed in the Rocky Mountains (Remington 1952, O'Neil 1980), and 1 in northeastern North America (Francis 1958). Snags were the second most prevalent structures for maternal dens (27%). In the Sierra Nevada, Simon (1980) documented a maternal den located in a large-diameter red fir (*Abies magnifica*) stub, Burnett (1981) described a maternal den in Montana in a 25 cm dbh lodgepole pine snag, and in Oregon and Washington, Raphael and Jones (1997) observed 13 dens in snags. Logs provided the next most common maternal den structures (18%). On Vancouver Island, British Columbia, 2 dens were located under stumps >1 m in diameter, 1 of which was surrounded by large logs (Baker 1992). Although Baker used the term "natal den site," it is not clear that either of these sites were used for parturition. Sixteen maternal dens have been reported in logs: 2 in Wyoming (Hauptman 1979), 1 in Ontario (Francis 1958), 2 in Maine (Wynne and Sherburne 1984), 10 in Washington, and 1 in Oregon (Raphael and Jones 1997).

In our study, marten used several artificial log structures for natal and maternal dens, including logs from the remains of old cabins and slash piles near the edge of cutover areas. These structures functioned very much as natural logs and blowdown. Marten used slash adjacent to uncut stands, and old cabin logs were within forested stands. Baker (1992) also reported dens in slash in second-growth sites, but the slash comprised large-diameter logs left from the former stand. Raphael and Jones (1997) found 9 dens in logging debris in Oregon and 2 in Washington.

Although middens composed roughly 12% of our maternal den observations and 55% of our natal dens, no other authors have reported the use of middens for either natal or maternal dens. The lack of middens being reported as den sites is surprising given that middens are important marten rest sites in Alaska (Buskirk 1984), Montana (Coffin 1994), and in the northern Sierra Nevada (Spencer 1987). This discrepancy may partly be due to differences in defining middens. We treated logs, stumps, and other den structures that were incorporated into intensive red squirrel feeding sites as middens. Defining dens as logs or stumps without acknowledging the midden itself ignores the importance of the midden to the den. In our study area, large logs were relatively common, but not commonly associated with middens. We feel that marten make a selection decision when choosing logs within middens versus logs not associated with middens.

The use of live trees as maternal dens in our study area was rare. However, roughly 33% of the maternal dens documented in other studies occurred in live trees (Grinnell 1937, Hauptman 1979, Wynne and Sherburne 1984, Raphael and Jones 1997). In general, marten appear to use cavities when denning in live trees, much as they do when denning in snags. Live trees that provide marten denning habitat tend to be larger diameter, older trees with woodpecker (Picidae) holes or natural cavities.

Ground dens have been described for marten, but they are rare (More 1978, Vernam 1987). Only 1% of our maternal dens occurred on the ground and without an associated structure.

Den-Site Characteristics

Our results indicate that structural characteristics associated with late-successional forests are important attributes for den sites selected by female marten. Marten selected natal den sites with more middens, more large-diameter logs, and greater canopy cover than occurred at random sites. Marten selected maternal den sites with more large-diameter logs and more large- and medium-diameter snags than random sites. That snags were more important as maternal den structures could account for the relatively higher selection coefficients for large- and medium-sized snags at maternal den sites. Although logs were used as den structures for natal and maternal dens, they were not among the most commonly used structures for either den type. Logs may supply structural complexity at ground level when not used as dens, and thus afford hiding and escape cover for females and kits around den sites.

Number of red squirrel middens was the most important variable for selection of both natal and maternal den sites. Although red squirrels are not restricted to late-successional forests, the well-developed middens marten used in our study area were often associated with large-diameter logs and other coarse woody debris. Such large, well-developed middens may be linked to coarse woody debris because of the presence of escape cover and feeding promontories provided by these structures (Pearson 1998).

Our data suggest that natal den sites had more well-developed middens, greater numbers of large, hard logs, higher percent canopy cover, more spruce and fir trees >20 cm dbh, and greater numbers of medium and large snags than maternal den sites (Table 1), which suggests that female marten may be more selective in choosing parturition sites than in choosing subsequent den locations. Although we were unable to test this hypothesis, this conclusion seems reasonable because marten select natal dens earlier in the year when conditions are colder and snow is present. This finding is generally consistent with Burnett's (1981) contention that marten are more selective in their choice of denning sites than resting sites. Because of the timing and energetic demands associated with each type of structure, we hypothesize that marten will be most selective of structural attributes when choosing natal den sites, followed by maternal den sites and resting sites.

The individual model for maternal den-site selection provided the best fit to the data, suggesting that all individual marten do not select den sites based on the same criteria. Differences in selection among individuals could also explain why 3 of the 9 marten did not appear to exibit selection within their home ranges. However, the scale at which selection occurs could also explain the lack of selection within home range exhibited by these 3 marten. As Johnson (1980) noted, animals make habitat-selection decisions in a hierarchical fashion. Accordingly, interpretation of selection within home ranges must include consideration of resource selections made at the broader scale of home ranges within landscapes. For example, the 3 females that did not exibit selection within their home ranges may have selected high-quality home ranges relative to the resources we measured. In this context, significant selection within a home range could indicate a poor-quality home range relative to the variables measured. In developing resource selection studies, multiple scales should be incorporated into study designs to better understand and interpret resource selection patterns.

Imprecise use of the terms natal den, maternal den, den, and den site has obscured our understanding of how structural attributes of habitats relate to marten parturition and kit rearing. The most common problem lies in use of the terms "den" and "den site" when referring to resting sites (sites with no direct connection to reproduction), or in failing to discriminate between den sites and resting sites when discussing site characteristics (e.g., Marshall 1948, 1951; Francis 1958, Francis and Stephenson 1972, More 1978, Burnett 1981, Spencer 1981, and others). A related problem is failure to discriminate between natal and maternal dens (e.g., Raphael and Jones 1997). These problems are exacerbated when uncritical references to these reports lead to their use as citations by other authors as they attempt to document additional statements about dens and den sites. For example, 2 important review papers, Clark et al. (1987) and Strickland and Douglas (1987), use the term natal den when citing Wynne and Sherburne's (1984) account of 2 maternal dens located in tree cavities. Natal and maternal dens play a critical role in marten recruitment, and marten in our study appeared most selective of structural attributes associated with natal dens. For these reasons, authors should (1) adopt and use precise terminology; (2) explicitly discriminate between resting, maternal den, and natal den sites; and (3) use the term "den structure" and "den site" to unambiguously distinguish between the specific den structure and the context within which these structures occur.

MANAGEMENT IMPLICATIONS

Our results indicate that marten den sites are characterized by attributes of late-successional forests such as large logs, and medium and large snags. In Wyoming, the trees necessary to provide the natal den structures we describe can take up to 250 years or more to develop. These findings are consistent with the prevailing view that optimal habitat for marten is extensive late-successional forest (Spencer et al. 1983, Clark et al 1987, Thompson 1991). We found natal and maternal dens in red squirrel middens and in large logs and snags that are characteristic of late-successional forest. Our findings are also consistent with Hawley's (1955) statement that mature forest types contain more denning sites than less mature types, and Bergerud's (1969) suggestion that the absence of large trees for denning could account for the absence of marten in certain parts of Newfoundland. Our findings are also consistent with Spencer et al.'s (1983) interpretation that marten require old-growth stands to provide dens and resting sites, and Thompson's (1991) contention that early-successional forests likely lack the natal den sites provided by large trees in old forests. We concur with Burnett (1981) in stressing the need for more research on the habitat requirements of denning females because existing information indicates that availability of den sites may limit some marten populations.

ACKNOWLEDGMENTS

We thank G. D. Hayward, S. W. Buskirk, and S. C. Minta for helpful manuscript reviews. L. L. McDonald and B. F. J. Manly provided valuable reviews of data analysis. We also thank G. R. Brown, W. D. Vansickle, and E. C. O'Doherty for their contributions to various phases of this research, and M. G. Raphael for initiating marten research on the study area.

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Received 11 October 1995.
Accepted 30 July 1997.
Associate Editor: McDonald.